



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

PLATE X.

- Fig. 14. *Hemileuca yavapai*. Spinulated dorsal tubercles of each thoracic segment, final stage.
15. *Gastropacha quercifolia*. Scales from dorsal tuft on second thoracic segment of the mature larva.
16. *Gastropacha quercifolia*. Flattened hairs from the lateral tuft of the second thoracic segment of the larva.
17. *Gastropacha americana*. Flattened hairs from the lateral tuft on eighth abdominal segment of the mature larva.

PLATE XI.

- Fig. 18. *Gastropacha americana*. Flattened hairs from the lateral tuft on second and third thoracic segments.
19. *Heteropacha rileyana*. Flattened hairs from the lateral tuft on the second thoracic segment of the mature larva.
20. *Acronycta hastulifera*. Flattened hairs.
21. *Clisiocampa americana*. Normal hairs, densely spinulated.
22. *Artace rubripalpis*. Freshly hatched larva. Bridgham del.

Note.—All the figures, except 1 and 22, were drawn by the author with the camera.

Energy as a Factor in Organic Evolution.

By John A. Ryder.

(*Read before the American Philosophical Society, April 7, 1893.*)

The fact that the energy developed by living bodies is correlated with cosmical energy is now a recognized canon of physiology. To give the proper emphasis to the part played by the energy developed within organisms, as a factor in the development of their own forms or *morphogeny*, is the purpose of the present paper. To define exactly the kinds of energy displayed and the mode in which its effects are produced in particular cases is another part of the subject to be dealt with. The definition of these subjects renders necessary the introduction of a few new terms, in order to avoid awkward circumlocution, to achieve brevity or directness of expression, and to eliminate the risk of indefiniteness in the use of words.

Hæckel very felicitously proposed the term *phylogeny* to express the fact that a certain tendency directed the drift or trend of development of a being along a line parallel with that of the series of forms ancestral to it. The being in the course of its development briefly recapitulated that of the ancestral series to which it belonged. This, in substance, is the famous fundamental *biogenetic law* first suggested by F. Müller.

Hæckel also proposed for the process of the development of the individual the term *ontogeny*, genesis of the individual being. The displays of energy, in time and space, controlling the process of development, both racial and individual, that is, the *phylogenetic* and *ontogenetic* processes, are now admitted on all hands to run more or less closely parallel. When old characters tend to reappear very early in *ontogeny*, it is explained that this is a case of reversion, atavism or *palingeny*. If, on the other hand, a new character tends to appear very late in the ontogeny, it is explained that it is because such a feature was late in appearing in the phylogenetic or racial history, it is therefore said to have arisen from comparatively recent variations of the type form, or to be *cænogenetic*. The registration upon the germinal matter of organisms of these developmental tendencies to reappear in a certain sequence and relation, in time and space, comprehends what is generally understood by the term *heredity*.

Hereditary phenomena are therefore *ontogenetic*, and in so far as the latter repeat an ancestral history they are *phylogenetic*. That is, the energies of individual development reflect or epitomize in the sequences and relations of their display those which have attended the evolution of the race.

Thus far the use of these terms, which have become current and well understood in biological literature, seems to be justified, in that they stand for a formula which is so largely true in spite of occasional discrepant facts that we must accept these words as brief or shorthand expressions for two great biological principles.

Adaptation of the organism to its conditions of life is now, as it always has been, a very difficult subject. Some have supposed it to be due to variation of the potentiality of the germinal matter derived from the two sexes, or to *Amphimixis*, and that the individual variations thus produced that were unfitted for survival were eliminated by natural selection. Others have maintained that there is more or less evidence of the occurrence of direct adaptation or adjustment of the organism to its surroundings with accompanying variation, and that consequently the energies developed within and without the organism had to do with the process of adaptation and the origin of variations. The development of adaptations was, therefore, according to this latter view, a resultant consequent upon the interaction of two sets of forces, namely, those developed within and also those developed without the organism. Natural selection in this case was also supposed to be operative as the agent eliminating the unfit. Weismann, Lankester and others have defended the first view. Hæckel, Cope, Spencer and even Huxley (the latter with some reserve, perhaps) have supported the latter opinion. Darwin himself was inclined to the last to ascribe a certain influence to external agencies, and also to use and disuse, in doing which he showed his leaning towards what has since his death been regarded as the more distinctly Lamarckian view of the origin of variations.

Prof. Cope has sought to establish a recognition of the factor of energy

as developed in the motions of organisms and their parts as an agency in the modification of the forms and proportions of their hard parts. In this he has distinctly followed Lamarck, Spencer and the writer, and to this agency he has applied the term *kinetogenesis*, which may also be written *kinetogeny* in order to make its Anglican spelling conform to that of the very useful terms proposed by Hæckel.

Unfortunately this term, *kinetogeny*, does not embrace a consideration of all the forms of energy that concern the problem of adaptation. My only reason, therefore, for invading this field of terminology is that there appears to be a need for another term which shall be more comprehensive and which shall apply to all the forms of energy involved in a study of adaptive processes, namely, the potential or static and the actual or kinetic. This will embrace both the energy of rest or equilibrium and that of motion or lack of equilibrium. The most general term that can be used for this purpose seems to be *ergogeny*, the etymology of which is apparent. This general term, *ergogeny*, will include not only *kinetogeny*, but also its antithesis, *statogeny*.

If an organism suffers morphological modification in consequence of the display of the energy of motion, any modification thus caused would be developed kinetogenetically. If, on the other hand, an organism were modified in such a way that the energies developed by it were in a condition of statical equilibrium, and, moreover, if its specific form depended upon the maintenance of such a statical balance, then any formal modification thus caused and maintained would be developed *statogenetically*. If it is meant that energy has been concerned in producing a certain modification without specifying the kind of energy, such modification may be said to have been produced *ergogenetically*. Concrete illustrations will, however, be necessary in order to give a clear notion of the very real difference that exists between the two processes, namely, *kinetogeny* and *statogeny*, embraced under the still more general term of *ergogeny*.

If the motion of the developing parts of an organism condition their structural modification in a definite and precise way, as in the case of the development of vertebral centra, of the vertical rows of scales on fishes, or the fractures across the fin rays of certain fishes, as I have shown elsewhere,* then the effects so produced are developed ergogenetically. In that such effects are the result of the expenditure of energy in the form of motion they are also developed kinetogenetically.

If, on the other hand, the process is one in which the energy developed is a consequence of growth itself, and is dependent merely upon the gross physical and statical properties of the living matter itself, such as the varying surface-tension of different parts of the surface of the plasma, then the problem becomes one, not of motion, but of the want of motion, of forces in equilibrium or a statical one. Such conditions of statical equilibrium of surface-tensional forces of the adjacent surfaces of the cells of

* "Proofs of the Effects of Habitual Use in the Modification of Animal Organisms," *Proc. Amer. Philos. Soc.*, Vol. xxvi, Nov. 21, 1889.

the early stages of segmenting eggs are known by the thousand to the skilled embryologist.

In that these cannot at first be overmastered by either phylogenetic or ontogenetic forces, or by both combined, proves that the forms so developed are, therefore, the resultants of the energy represented by the phylogenetic and ontogenetic or the sum of the hereditary forces working in antagonism against a recurring statical condition of the substance of the germ. This statical condition reasserts itself at the close of every segmentation, so that there is a recurrent conflict between these two sets of forces at every step of development. In fact, the round or oval form of the egg is a statical condition of the germinal mass dependent wholly or partially upon its own surface-tensional properties. That this is gradually overcome in the course of the ontogenetic process is well known, but it is also a fact that no known form of animal or vegetable development is exempt from the influence of the interference of statical forces of equilibrium, mainly those of surface-tension. In so far, therefore, as the form of the early stages of the development of an embryo are thus interfered with, such modifications are statogenetic. The great generality of this principle, therefore, becomes apparent. The generality of statogeny is, in fact, coextensive with that of phylogeny and ontogeny. But this is not all. Every statogenetic state alternates with a kinetogenetic state, since every new statogenetic condition is heralded by a kinetogenetic one. It is this incessant organic and organizing seesaw of processes that is comprehended under the still more general term of ergogeny.

Such must, therefore, be my excuse for adding this new set of terms to those already in use, since they represent a series of processes of such universality as to be of an importance second only to those of phylogeny and ontogeny. To illustrate in detail the great variety of phenomena with which ergogeny and its forms, kinetogeny and statogeny, have to deal would much transcend the purposes of this paper. Only sufficient additional examples will therefore be given to show the far-reaching character of these principles.

In the motion of *Amœba proteus*, kinetogenetic phenomena either alternate rhythmically with statogenetic phenomena, or perhaps more correctly, both constantly accompany one another in the course of the movements made by this very simple organism. The chemical processes within the *Amœba* by means of which its surface-tension is constantly being disturbed are kinetogenetic, since this equilibrium or statical balance of the plasma is thus recurrently overthrown. This leads to a temporary rupture of the surface layers of molecules and an intrusion of new molecules from within to repair the rent. When this is accomplished a statical equilibrium is temporarily restored only to be followed by a recurrence of motion or overthrow of statical equilibrium. This leads to the more or less fitful or interrupted motion seen in these organisms. These alternating and conflicting processes also determine the figure of the organism at every instant, so that ergogeny becomes, in the lowest forms, through its elementary

types of kinetogeny and statogeny, form-determining or morphogenetic. The development of the figure of the body of *Amœba proteus* is also partially conditioned by cohesion to adjacent surfaces, and is also, to some extent, pulled upon as a semifluid mass by gravity and flattened. The vortical flux of its own particles through themselves also elongates it in the direction of its own motion. This causes the anterior end of the organism to present a tense, rounded outline, while its posterior end is wrinkled, papilliform or uneven. The vortical flux of particles in the centre of the body of the organism flow fastest while they gradually move slower towards the surface where the ultimate and outermost layer is at rest. Thus in every detail of its morphology do we discover that Amœba is absolutely the creature of energy conditions. Its shape at every instant of its existence is determined ergogenetically as we may speak of the form-conferring forces developed from within as distinguished from those of gravity, adhesion and cohesion that are operative from without. Even the ideally perfect form of vortex motion of the particles of its substance is disturbed and distorted by the interaction of this complex set of forces. Moreover, since the physical properties of the different species of Amœboids are very different, their kinetogenetic and statogenetic characteristics differ correspondingly, so that their behaviors are very different for this reason. The profound differences of form presented by their pseudopodia are to be partially accounted for on this ground, and partially on the ground of the differing physical constitution of their substance.

The phenomena of motion of plasma or cells may be generally comprehended under the term *cytokinetic*, their statical conditions under the term *cytostatic*. In the same way the active and resting stages of nuclei may be regarded as *karyokinetic* and *karyostatic*. The motion and rest of the centrosomes of cells may be named as their *astrokinetic* and *astrostatic* conditions. These six terms, one of which is already in use, are proposed in order to connect the phenomena of cell division with ergogeny in general. The origin of the motion of the Amœba is to be sought in its own plasma; it is therefore cytokinetic. The alternating periods of quiescence of Amœba are cytostatic; its spherical form in the encysted condition is the result of a perfect cytostatic equilibrium in every direction. These results are also ergogenetic; that is, the changes of configuration due to motion are kinetogenetic; those due to a condition of temporary statical equilibrium are statogenetic.

Osmotic processes in combination with surface tension and reciprocal pressures developed against adjacent structures develop the most manifold changes of configuration. If osmotic pressure is the same in every direction within a cell or a mass of cells, a spherical figure results such as that of Volvox. If, on the other hand, the equal internal pressures are antagonized from without by unequal pressures at different points corresponding modifications of figure are developed. This is illustrated in the most manifold ways in the cells of plants and animals. Such modifications thus caused are largely statogenetic.

If motions of hard parts upon each other tend to alter or deform the modeling of the surface in a particular way, as seems to have been the case with teeth, the process is kinetogenetic. If the basal part of the conical surface of a pointed tooth have its enamel organ folded under constraint during growth in a conical matrix into which it expands by growth more rapidly at its basal region than the walls of this matrix expand, the result is partly kinetogenetic and partly statogenetic.

If the development of a blastoderm be conditioned by surface and interfacial tension in such wise as to cause it to conform to the configuration of double curvature of the yolk mass upon which it extends itself, the result is mainly statogenetic. If an embryo be pressed down into the blastoderm as the result of constraint from above during its growth, and the surrounding non-embryonic area is thus caused to be reflected over it more and more as growth of both embryo and blastoderm go on, an amnion is developed. This process is kinetogenetic so far as the growth and reflection of the blastoderm is concerned, but statogenetic in so far as the permanent molding and retention of the figure of the amniotic cavity is concerned. If fin-rays are fractured or segmented in a regular fashion and in response to the exigencies of the motions of the fin, such a result is kinetogenetic. If the calcifiable matrix developed about a notochordal axis be regularly segmented at points alternating with the intervals between the myotomes by the agency of the motions to which such an axis is subjected during use, the result is again kinetogenetic. If an originally globular egg be distorted into an ovoidal body within a tubular oviduct due to circular pressure, as happens in birds and insects, the result is almost purely statogenetic. An empirical mathematical formula may therefore be written for every variation in the shape of the common hen's egg for a curve which shall account also for its shape.

If, as in the case of the double monsters developed in meroblastic eggs due to karyokinetic disturbances, there is a strong interfacial tensional attraction between the germ and yolk substance, it is impossible to shake the first blastomeres apart as in the case of holoblastic eggs, so that fused embryos or monsters only can be produced from such meroblastic ova. Such a result is statogenetic, that is, statical conditions in the meroblastic egg so far override the ontogenetic processes that fused monsters only are here possible, whereas in holoblastic ova in which the blastomeres can be completely separated two or more distinct embryos can be produced from what had begun its development as a single embryo.

So universal is this interference of the statical conditions of the plasma of segmenting ova with the ontogenetic processes, that not a single metazoan organism can be named the development of which is not thus marred in some way or other. It is often a long time relatively after development has begun that there is any obvious delineation of the embryo. In fact, this cannot take place until the statical energies of surface-tension which have kept the egg globular are overridden. In so far as the ontogeny of any organism is marred by statical conditions of energy-display, its em-

brionic form is also modified. In so far as such statical interference affects the figure of the organism they are morphogenetic or form-determining. In so far the figure of a developing being is disturbed or modified by statical agencies its figure may be said to be subject to statogenetic influences. No existing larval form has escaped the influence upon its own shape of a constantly active statical equilibrium of its own substance. There is, therefore, a constant struggle going on during development between the phylogenetic and ontogenetic forces, determining the sequence and relations of the successive cleavages of the egg and the statical equilibria that obtain amongst its several parts. Statogenetic processes are, therefore, as constant and universal as the phylogenetic and ontogenetic. One may even go so far as to say that possibly the relations thus tending to be established by statical conditions may tend to become transmissible as hereditary tendencies. Such indeed is the view upheld by Prof. E. B. Wilson in his remarkable paper on "The Cell-lineage of Nereis."* I have myself seen no less than three consecutive recurrences of the same statical conditions in a fish egg, none of which can, for this reason, be definitely proved to be purely ontogenetic.

The facettèd eyes of insects are usually hexagonal, but not invariably so. I have found triangular, quadrangular and hexagonal facets in the eyes of *Tachinus*. Now these different forms are due to disturbances of the statical conditions obtaining between the individual ommatidia during growth of the eye. If the pressure is the same from every direction laterally during growth, a cylindrical eye would result. If the lateral pressure is the same from six points at equal distances apart around each eye, the regular hexagon will result; should any two opposite pairs of the six pressures be less than the pressures from the other two pairs irregularities in the hexagons will appear. If cylinders are grouped so that the side of every one touched the sides of six others, which may be done by bringing their tops into rows in three directions, and if now each cylinder be increased in diameter, there will be pressure developed in six directions diverging at equal angles of 60° from one another, a hexagonal configuration of the ends of the cylinders would ultimately result, provided they were formed of plastic material. The same thing sometimes happens when a plastic and nearly homogeneous mass cools and contracts, when cracks appear in the mass generally dividing it into pentagonal and hexagonal prisms, as happened in case of the cooling of intruded mass of molten basalt in the Giant's Causeway in Ireland. A series of cylinders arranged so that every one shall touch six others is also most economical of space, and in the processes of growth is the natural result of a statical equilibrium due to equal pressure from six directions in a plane. If a series of cylinders be brought into rows in two directions only, and so as to touch their neighbors at only four points, quadrangular columns would result were the diameter of every cylinder increased against four others, provided all were composed of plastic material. In these ways have the

* *Journ. Morphology*, Vol. vi.

various forms of the facets of the compound eyes of insects arisen. So too the reciprocal marginal interference of the growth at six equidistant points of the scutes of such forms as the extinct Glyptodonts, has developed in such scutes a hexagonal configuration. In these cases growth is the kinetogenetic factor, and the statogenetic factor is the struggle to bring about an equilibrium of marginal pressures during growth, as a consequence of which a hexagonal figure results.

The development of a cylindrical form of the body is also a case where an equilibrium is concerned that is largely statical in character. The tense condition of its fluid-containing cavities, such as the alimentary canal, will confer upon such an organ a cylindrical configuration; so also in the case of blood vessels. It is indeed probable that the very form of the blood corpuscles or disks is discoidal in virtue of a statical equilibrium of their substance within the fluid plasma in which they are immersed, and that there is a double vortical flux of the substance of these disks from the centre to the periphery on both faces, or the reverse. This vortical flux is probably maintained by the exigencies of metabolism and calls for the incessant exhibition of a tendency towards a condition of statical equilibrium. In this way we may conceive that the thousands of millions of red blood disks coursing through our vessels are enabled to not only maintain their flattened configurations, but to also thus greatly increase the areas of their surfaces and be thus rendered more efficient agents in the processes of oxidation and deoxidation. Here is a statical condition, as we may suppose, that has been adaptively developed through the direct expenditure of energy, by the matter of the corpuscle itself. In other words, our red blood corpuscles have, in the first place, and with the utmost probability, acquired their present configuration ergogenetically. If this is true in the case of the blood disks of ourselves, it is probably also true of the blood disks of all other forms.

The globular form of the egg is a statically developed condition, so is that of the more or less nearly globular morula and also of the blastula; but in the latter internal osmotic pressure is also a factor. Even the brain shows in its earliest form the tendency to develop as vesicles under statical conditions. Here its growth is the kinetogenetic factor, and the tendency for the hemispheres to be at first globular vesicles is owing to the statical influence of the substance composing their walls. Later, as these vesicles grow, they press upon each other along the median line when they present a flattened aspect towards one another from the operation of the same causes, and we at last have developed the "hemispheres" of anatomists. In this way it results that a single somewhat globular body is formed, made up of two halves. Under constraint within the membranous cranial walls the latter conform to this pressure of the growing brain-globe within and conform to its shape, so that a somewhat globular cranium results. Following in detail the evolution of the fissures of the brain, even these are developed kinetogenetically through growth; the pallium or cortex under restraint within the skull grows and shows a tendency to

have its wall folded into ridges, with intervening fissures that tend, for assignable mechanical laws, to join one another at an angle of 120° , as first pointed out by the late Dr. A. J. Parker, and, as it seems to me, correctly attributed by him in part to ergogenetic influences. It may also be shown that the heart, in the course of its development, gives evidence of being subject to the morphogenetic influence of ergogeny.

The spiral or torsional form of many of the articular faces of the ends of bones in the limbs of terrestrial vertebrates can probably be shown to be associated with the development of torsional stress in locomotion. That such torsional stress is actually developed during the locomotion of terrestrial vertebrates has been conclusively proved by Prof. Allen from a careful study of the work of Muybridge upon animal locomotion. Upon every hand, therefore, there is evidence of structure that has been developed in conformity with the conditions of the expenditure of animal energy. I have myself called attention to the fact that digital reduction first began in the hind limbs or in those subjected to the greatest stress, in leaping, by land vertebrates. The forelimbs show this tendency later and in conformity with the fact that they cannot become the channel for the dissipation of such large amounts of energy, impulsively, as the hind ones. Digital reduction and specialization is therefore to be regarded as having been induced and begun ergogenetically.

In the course of other work I have had occasion to call attention to the fact that the foundations of the skeleton were in every case laid down in certain comparatively inactive, or, as I have elsewhere expressed it, ametabolic tracts. These tracts were either external, protective non-plasmic envelopes or they were developed between the organs. In both cases they tend to take the form of intercellular or circumcellular matrices, or as matrices laid down between organs. Metabolism is *nil* in them everywhere because of the non-plasmic and the non-metabolic character of their substance. Such matrices, therefore, present from the lowest protozoa up to the highest metazoa tolerance of inert foreign matters within their substance. Such matrices being colloid, they often attract inert calcareous or silicious matters that are held in solution in the circulating fluids as deposits, just as such deposits are seized and held under laboratory and non-vital conditions by colloids in the presence of hypersaturated solutions. In other words, there is here a tendency to revert to a statical condition on the part of these inert salts, which thus tend to crystallize within such a matrix and within the living body. These matrices are thrown out as a protection, or as the result of irritation of cell tracts, or to increase the volume of an organism; the colloids of which they are composed attract the inert calcareous or silicious salts that pass through the living and adjacent plasma and a statical equilibrium is thus restored. The skeletal matrix thus calcifies, as we express it, whereas the truth is that we are probably dealing with a phenomenon that differs but little in its essential nature from one that may be imitated in the laboratory. The process is one that ultimately develops a statical equilibrium when the

matrix is saturated with inert silicious or calcareous materials. This may be especially well shown in regard to the wonderfully complex shells of Radiolarians, Foraminifera, the spicules and skeletons of sponges, the shells of the eggs of birds, the calcification of bone and cartilage, etc. I therefore very much question whether there is a single skeletal structure anywhere to be met with, the development of which does not take place in some measure statogenetically. Especially is this true of the configuration of the skeletons of such complex objects as Radiolarians, Foraminifera, etc., where surface tension coöperating with the process of the gradual statogenetic saturation of the matrix gives to them their wonderful complexity and beauty. While such phenomena as those of the genesis of the heterocercal or upwardly deflected condition of the axis in the tails of fishes, or the downwardly deflected condition of the axis in Ichthyosaurs are almost purely kinetogenetic, the multiplicity of factors concerned, statogenetic as well as ontogenetic and phylogenetic, must always be considered and each given its due weight and importance in achieving the morphogenetic result. That there is an absolute conflict between statogeny and kinetogeny on the one hand, and of phylogeny and ontogeny on the other, in the case of the development of the ova of multicellular forms admits of no doubt. All metazoa pass through larval stages in which the statical condition of equilibrium of the plasma of the egg is gradually, in a great measure, overridden by the hereditary energies represented by phylogeny and ontogeny. That there still remain traces of the effects of kinetogeny and statogeny in the adult organism cannot be denied in view of the facts to be derived from the shapes of tissue elements, and even of organs, as the foregoing paragraphs show.

These few observations and reflections will, I think, at least make it clear that the terms *ergogeny*, and its forms of *kinetogeny* and *statogeny*, are justified, and that they stand for what constitutes a very important part of the machinery of organic evolution, the generality and importance of the influence of which is certainly not less than second to that of phylogeny and ontogeny. The energy factor or ergogeny left entirely out of consideration must therefore seriously cripple the symmetry and completeness of any general theory of organic evolution.

APPENDIX.

The introductory chapters to Hæckel's great work on the Radiolaria, forming part of the series of *Challenger Reports*, contains much that is suggestive in relation to the subject of this paper. Also papers by Dreyer and others in the *Jenaische Zeitschrift*, in reference to the ergogenetically developed forms of the tests of Radiolarians, Rhizopods and Foraminifera. The botanists have long since appreciated the importance of this subject, and Berthold's *Protoplasmechnik* is an especially suggestive work. Sachs has also contributed to the subject. Much that is suggestive is also to be found in the *Principles of Biology* of Herbert Spencer, though his facts

are not invariably to be depended upon, owing to the very different interpretations now to be given many of them. Papers by Cope on the mechanical development of the structure of the hard parts, teeth and joints, are to be found in the *American Naturalist*, *Journal of Morphology* and *Proc. Amer. Philos. Soc.* Prof. Hyatt has also published several important papers on this subject, especially in reference to Molluska. Suggestive papers have also been published in this connection by Dr. W. H. Dall, while Lang has considered the development of the shells of univalve mollusks from a mechano-physiological standpoint in his *Lehrbuch d. Vergleichenden Anatomie*.

Purely physical papers by Plateau, Mensbrugghe, Quincke and others are also important as well as the experimental and biological results published by O. Bütschli and H. Virchow.

The subjoined list of papers by the author of the foregoing paper embraces the principal part of what he has published upon the ergogenetic development of morphological characters in the animal kingdom :

On the Laws of Digital Reduction, *Am. Naturalist*, 1877, pp. 603-607. *Nature*, xvii, 1877, p. 128.

On the Mechanical Genesis of Tooth-forms, *Proc. Acad. Nat. Sciences*, Philadelphia, 1878, pp. 45-80 (Abstr. by C. N. Peirce).

Dental Cosmos, xx, 1878, pp. 465-472.

Further Notes on the Mechanical Genesis of Tooth-forms, *Proc. Acad. Nat. Sciences*, Philadelphia, 1879, pp. 47-51. Review of by E. D. Cope, *Am. Naturalist*, 1879, pp. 446-449.

On the Origin of Bilateral Symmetry and the Numerous Segments of the Soft Rays of Fishes, *Am. Naturalist*, xiii, 1879, pp. 41-43.

The Gigantic Extinct Armadilloes and Their Peculiarities, With a Restoration, *Pop. Sci. Monthly*, xiii, pp. 139-145. 4 figs. [Discusses the mechanical genesis, degeneration, and coalescence of vertebral centra.]

The Significance of the Diameters of the Incisors of Rodents, *Proc. Acad. Nat. Sciences*, Philadelphia, 1877, pp. 314-318.

On the Position of the Yolk-blastopore as Determined by the Size of the Vitellus, *Am. Naturalist*, 1885, pp. 411-415.

On the Availability of Embryological Characters in the Classification of the Chordata, *Am. Naturalist*, 1885, pp. 815-819 and 903-907.

On the Genesis of the Extra Terminal Phalanges in the Cetacea, *Am. Naturalist*, 1885, pp. 1013-1016.

An Outline of a Theory of the Development of the Unpaired Fins of Fishes, *Am. Naturalist*, 1885, pp. 90-97.

The Origin of the Amnion, *Am. Naturalist*, 1886, pp. 179-185.

On the Origin of Heterocercy, etc., *Ann. Rep. U. S. Com. of Fish and Fisheries* for 1884, pp. 981-1085, Pl. ix, 1836.

A Theory of the Origin of Placental Types, etc., *Am. Naturalist*, 1887, pp. 780-784.

On the Homologies and Early History of the Limbs of Vertebrates, *Proc. Acad. Nat. Sciences*, Philadelphia, 1887, pp. 344-386.

On the Development of the Cetacea, etc., Ann. Rep. U. S. Com. of Fish and Fisheries for 1885, pp. 427-485, Pl. iii, 1887.

A Physiological Theory of the Calcification of the Skeleton, Proc. Am. Philos. Society, xxvi, 1889, p. 9.

The Polar Differentiation of Volvox, etc., Am. Naturalist, 1889, pp. 218-221.

The Quadrate Placenta of *Sciurus hudsonius*, Am. Naturalist, 1889, pp. 271-274.

The Origin of Sex, etc., Proc. Am. Philos. Society, xxviii, 1890, pp. 109-159.

The Placentation of the Hedgehog and Phylogeny of the Placenta, Am. Naturalist, 1890, pp. 376-378.

A Geometrical Representation of the Relative Intensity of the Conflict Between Organisms, Am. Naturalist, 1892, pp. 923-929.

On the Mechanical Genesis of the Scales of Fishes, Proc. Acad. Nat. Sciences, Philadelphia, 1892, pp. 219-224.

The Principle of the Conservation of Energy in Biological Evolution ; A Reclamation and Critique, Proc. Acad. Nat. Sciences, Philadelphia, 1892, pp. 455-468.

The Inheritance of Modifications Due to Disturbances of the Early Stages of Development, Especially in the Japanese Domesticated Races of Gold-carp, Proc. Acad. Nat. Sciences, Philadelphia, 1893, pp. 75-94.

The Mechanical Genesis of the Form of the Fowl's Egg.

By John A. Ryder.

(Read before the American Philosophical Society, April 21, 1893.)

The configuration of the outline of the hen's egg is determined apparently by mechanical means while the egg-membranes and shell are in process of formation within the oviduct.

The conditions, after the passage of the ovum or yolk proper into the oviduct, seem to be about as follows :

1. In the upper part of the oviduct the albumen is laid down upon the yolk by the activity of the albumen-secreting structures forming the wall of the duct. This albumen is laid down in successive layers, as is proved by the structure of the albumen and chalazæ, when these are coagulated by heat and then cut into thin sections. This lamination of the albumen is a result of the mechanical relations that the yolk sustains to the surrounding albumen-secreting surfaces, and this structure of the albumen is mechanically caused. The chalazæ are produced as the first deposits of albumen in the oviduct behind and in advance of the yolk. The twisting of the chalazæ is mechanically caused for the reason that the twist of the chalaza